Volume 13 Number 7 **3 May 2026**

The Taxonomic Report

OF THE INTERNATIONAL LEPIDOPTERA SURVEY

ISSN 2643-4776 (print) / ISSN 2643-4806 (online)

A new subspecies of *Papilio indra* (Papilionidae) from the West Desert of Utah, USA.

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ZooBank registration: urn:lsid:zoobank.org:pub:021FBED9-6B41-414D-A571-8C88A4654AFD

Abstract: *Papilio indra bonnevillensis* is a new described subspecies partly based on taxonomic rearrangement of its larval host plant reproductive phenology relative to Wasatch Range nominate *Papilio indra*. It is geographically isolated in Utah's West Desert from populations of ssp. *nevadensis* to the west and ssp. *calcicola* to the south. In addition to phenological differences compared to these two subspecies, it merits description based on host *Lomatium depauperatum* which recently speciated from *L. grayi*, neither of which is used as host by other subspecies of *P. indra*. The evolution of new host *L. depauperatum* is briefly described with how it affected development of this new Indra subspecies. New ssp. *bonnevillensis* is described along with its geographical range and life history.

Additional key words: *Lomatium depauperatum.* Pleistocene Lake Bonneville, Canyon Mountains, ecogeographical race.

INTRODUCTION

Considerable phenotypic variability has been recognized in Indra swallowtail butterflies (*Papilio indra* Reakirt 1866) in western North America and over several years a number of geographic races have been named: *pergamus* (Edwards 1874); *minori* (Cross 1937); *kaibabensis* (Bauer 1955); *fordi* (Comstock and Martin 1955); *martini* (Emmel & Emmel 1966); *nevadensis* (Emmel & Emmel 1971); and *phyllisae* and *panamintensis* (Emmel 1981). In more recent years the list of subspecies expanded again with the addition of three new races: from northern California near Mount Shasta, *shastensis* (Emmel & Emmel 1998); from southern California near Needles, *pygmaeus* (Emmel et al. 1998); and from near Lake Mead, Nevada, *calcicola* (Emmel & Griffin 1998). This brought the total named races to twelve (**Fig. 1**).

To understand the significance of new Indra subspecies *bonnevillensis* being proposed and described here, we first describe how it was discovered in relation to its recently speciated and described host plant *Lomatium depauperatum* (Alexander et al., 2018).

The existence of Indra swallowtail populations in the eastern Great Basin Desert ranges (West Desert) of Utah was initially discovered in 1985 by the late COL. Clyde F. Gillette in the Cricket Mountains of Millard County, Utah. He initially called this newly found *Papilio indra* population "bonnevillei", and it soon came to be known by local collectors as "West Desert Indra" (Stout, 1997). But Mr. Gillette never officially named and described it. The larval host is *L.* grayi which past floras had listed as a complex of morphotypes with wide distribution across 8 western states within three floristic regions involving two named subspecies, *L. grayi grayi* and *L. grayi depauperatum* (**Fig. 2**).

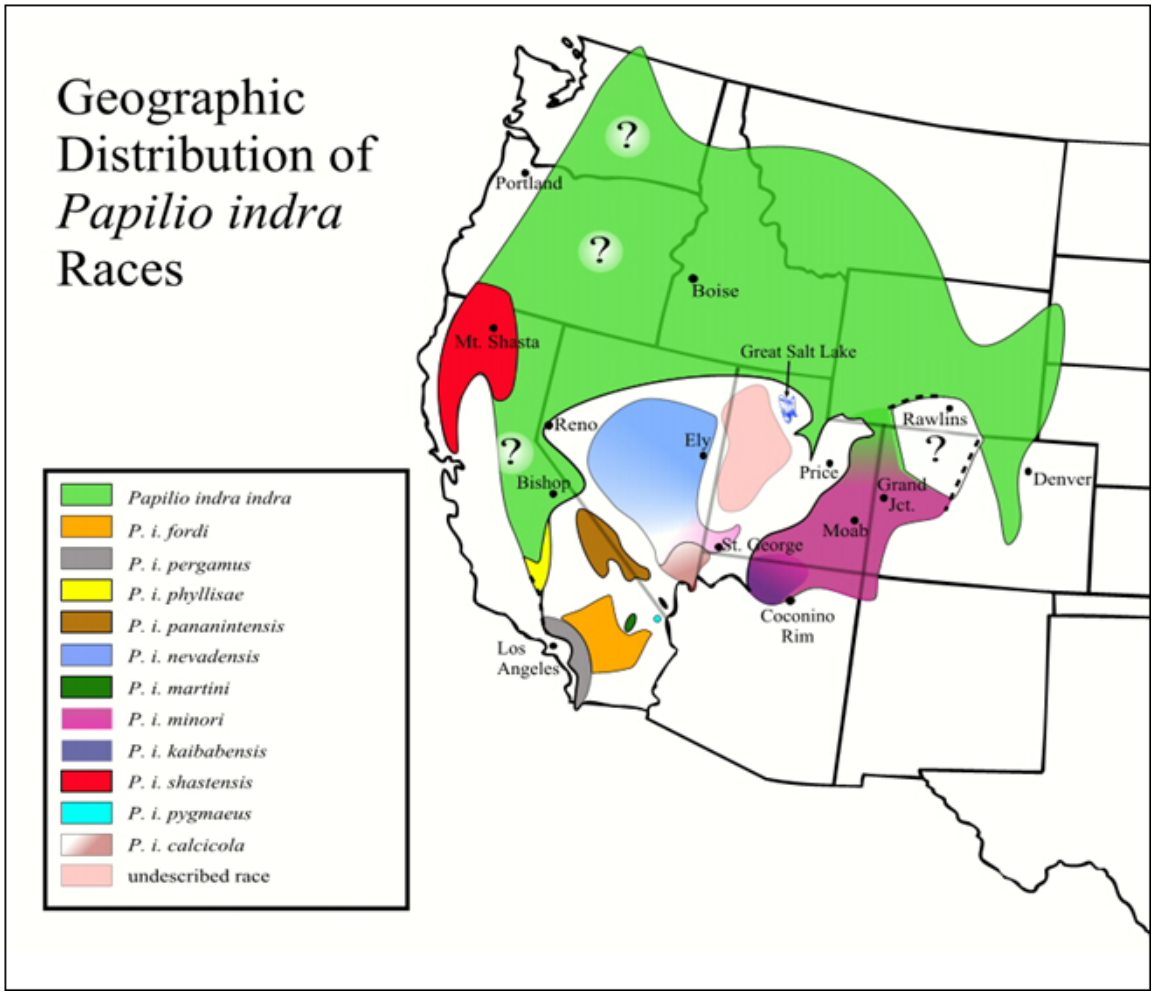

Fig. 1. Distribution of described races of *Papilio indra.*

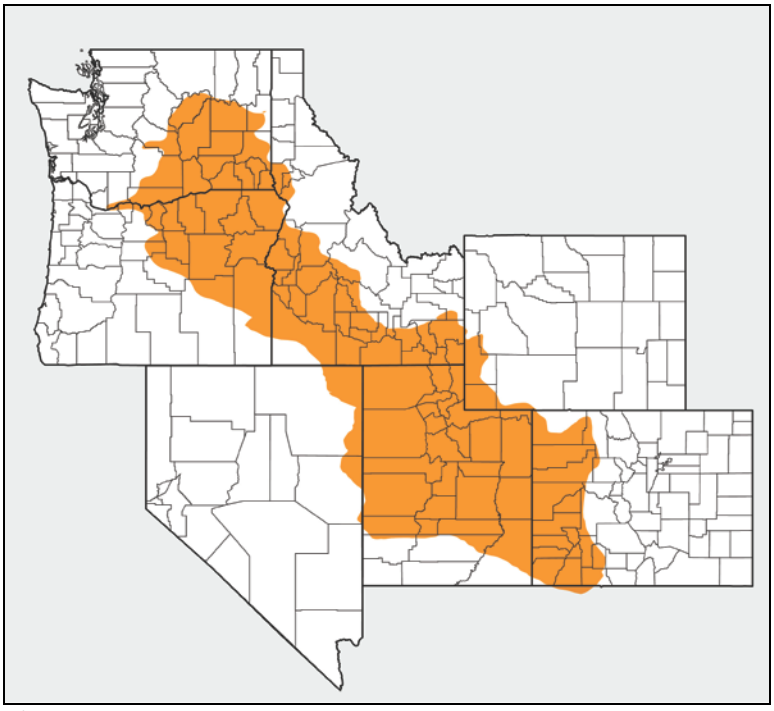

Fig. 2. Former *Lomatium grayi* range.

The variety in the Cricket Mountains had been listed as *L. grayi depauperatum*. Within this physiographic region, remnant of Pleistocene Lake Bonneville, Whaley in 2012 encountered two phenotypically distinct *L. grayi* plants growing side-by-side in Oak City Canyon, Millard Co., Utah. One was *L. grayi depauperatum*, the other *L. grayi grayi* with no intermediate phenotypes growing in the vicinity. This finding hinted that the two taxa had isolated gene pools and were different species

.

Earlier in 1999 Whaley discovered that Pacific Northwest Indra swallowtail butterflies were using larval hosts that botanists had afore referred to as *L. grayi*, but these plants were very different from those to the south in Utah and Colorado. Through morphometric analysis Drs. Jason Alexander and Wayne Whaley separated these *L. grayi* morphotypes into 3 new species. The Pacific Northwest populations were split into new species, *L. klickitatensis* endemic to the Klickitat River region in Washington, and *L. papilioniferum* distributed through eastern Washington, eastern Oregon and western Idaho. Likewise, the *L. grayi* populations of Utah were split, by elevating all Nevada and Utah populations of *L. grayi depauperatum* to species, which separated them from typical *L. grayi* of the Wasatch Range eastward into western Colorado. Based on the original description of taxon *L. grayi* the type locality was retained within Utah populations near Salt Lake City (Alexander et al., Ibid). The *L. grayi* of Utah, SE Idaho, SW Wyoming and Western Colorado are not hosts to *Papilio indra* populations (**Fig. 3**).

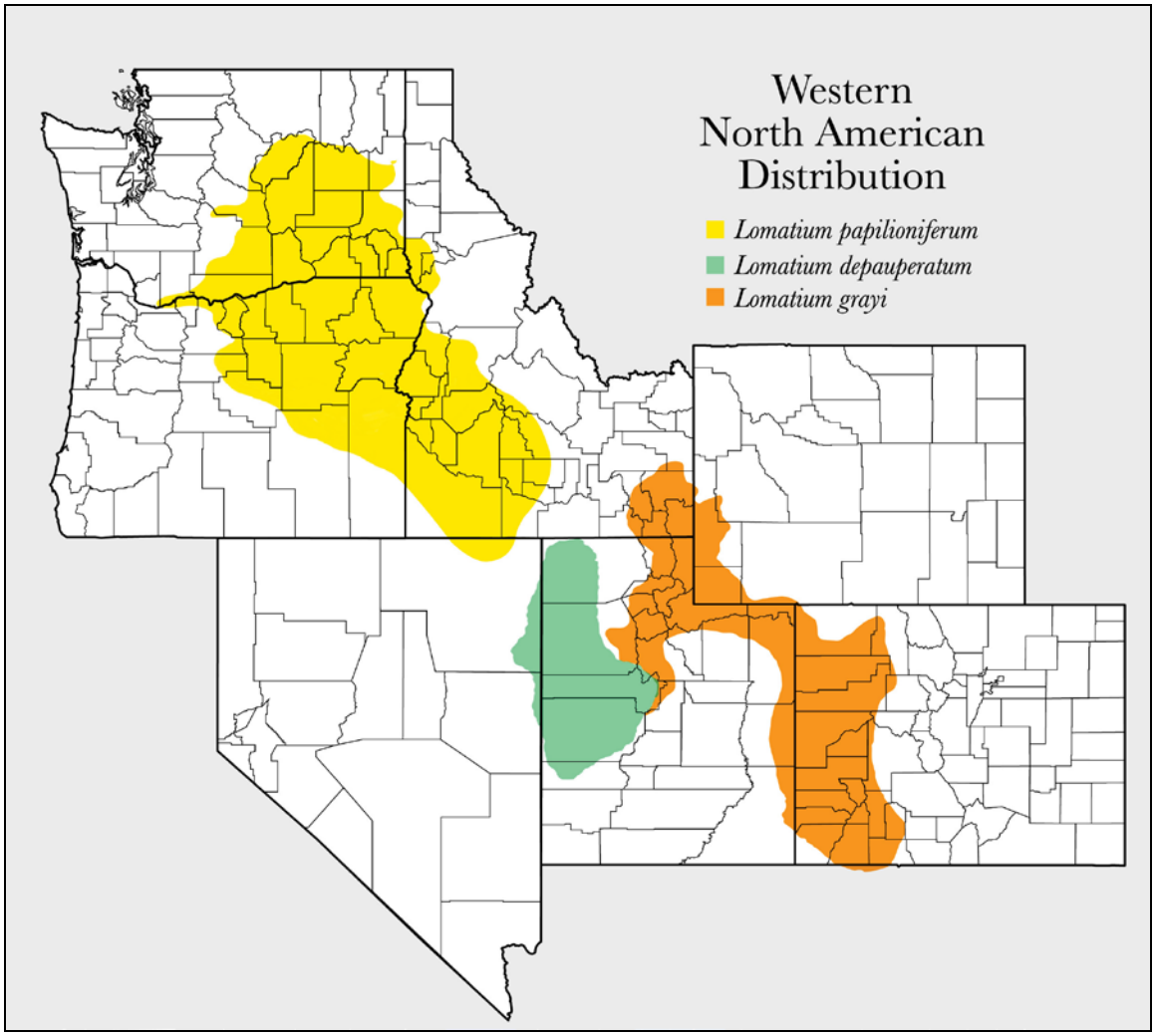

Fig. 3. New *Lomatium* species ranges (Alexander et al. 2018).

The flight phenologies of nominate *P. indra* in Utah's Wasatch Range and *bonnevillensis* of Utah's West Desert are very different and elevation specific niche requirements of potential larvae host plants factored into the historic separation of these two *indra* subspecies**.** This suggests that *P. indra* switched hosts at some point after the speciation event that gave rise to *L. depauperatum* from *L. grayi*. Eventually new Indra subspecies *bonnevillensis* had-become synchronized with *depauperatum*'s reproductive phenology which was well adapted to the hot, dry low elevation desert environments of western Utah's Great Basin; it being fully leafed out as early as March, and well into fruiting stage by April. Unlike most *P. indra* host plants, it was drying out as early as May, faster than any other known host of Indra swallowtails. This required *P. indra* females to fly and begin ovipositing as early as March, a time when other local host plants, including high elevation Wasatch Range Indra host plants, *L. graveolens* and *Cymopterus hendersonii*, were still dormant and unavailable to them. Nominate *P. indra* populations of the Wasatch Range genetically adapted to these high elevation Apiaceae species for their larval hosts characteristics and these Indra likely retain some taxonomic characteristics of Reakirt's original *P. indra* description – "upper surface deep blackish brown with two macular yellow bands one below the cell, the other submarginal in both wings" (Reakirt, 1866).

The flight period of ssp. *bonnevillensis* is late March to mid-April and is highly dependent upon Winter season moisture, while flight period of nominate *P. indra* of Wasatch Range eastward into Colorado depends upon elevation, snowfall, and larval host availability. For example, 10 June 2011 the Crawford Mountains, Rich County at ca. 6500 ft. we found many fresh adults and dozens of freshly laid eggs on *Cymopterus terreinthinus* var. *calcareus*. Example, at Bear River Mountains of Cache County and various isolated locations along the Wasatch Front nominate *P. indra* uses *Cymopterus terrebinthinus* var. *calcareus* at elevations of 5500 to 7000 ft. and flies from mid-May to late July. During May along Blacksmith Fork Canyon, Cache Co., UT, at about 5200 ft., we frequently found dozens of fresh nominate *P. indra* on the wing. The host at these locations was also *Cymopterus terrebinthinus* var. *calcareus* growing along canyon bottoms. On the other hand, above 8000 feet in the Wasatch Mountains nominate *P. indra* utilizes larval hosts *L. graveolens* and *C. hendersonii* and here its flight period varies from late-June to September.

Today the life cycle of *P. indra bonnevillensis* of Utah's West Desert has become highly synchronized with the reproductive phenology of its only host plant, *L. depauperatum*. Even when reared in artificial environs of captivity *bonnevillensis* ecloses in timing with the phenology of its native larval host plant. It appears then that *P. indra bonnevillensis* has evolved exceptionally close ties with host *depauperatum*, separating it from nominate *P. indra* of the nearby Wasatch Range. Because Utah's West Desert *L. depauperatum* is the sole native larval host of new Indra subspecies *bonnevillensis*, and because it is so tightly adapted to it, it has the earliest flight period of any known *P. indra* populations of similar latitudes and elevations. Adults fly from March to late April depending on flux in yearly Winter season moisture and temperature. Those *P. indra* populations that are on *L. depauperatum*, for the most part, emerge all at once; or at least more together than those on other host plant species. Maybe they are more synchronized on *L. depauperatum* because the plant dries up quickly and larvae would die if eggs were laid too late. However, with Utah's "fickled" weather in the lower deserts (e.g., June snows) we more than once found dead adults in March. Because of the reproductive phenology of *L. depauperatum* and because *P. indra bonnevillensis* is exceptionally synchronized with it, this ssp. is univoltine and the best time to see good numbers of them is early to mid-April.

As previously noted, *P. indra* does not naturally use *L. grayi* as a larval host. By our experience the twelve previously named *P. indra* subspecies cannot be successfully reared on either *L. grayi* or *L. depauperatum*, although ssp. *bonnevillensis* can be laboratory reared on either. This supports that *L. depauperatum* only recently evolved from *L. grayi* and that *bonnevillensis* adaptively evolved to it and is capable of de-toxifying any harmful chemicals of *L. grayi*, while other *P.* indra subspecies cannot. Essential

oils of these plant taxa emit strong essences of celery (e.g. essential oils limonene, myrcene, and β-phellandrene), while most *P. indra* host plants emit essences of citrus and pine which may be involved with host plant recognition and choice by females.

In Utah, populations of two *P. indra* subspecies are found within the known geographical range of taxon *L. grayi*, (**Fig. 3**), but it is not used as larval host by either of them. In northern Utah, nominate *P. indra* uses high elevation *L. graveolens* and *L. hendersonii*, or lower elevation *C. terebinthinus* var. *calcereus* as hosts, while in the southern portions of the plant's range *P. indra minori* utilizes host plants *C. terebinthinus* var. *petreus*, *Lomatium junceum*, *L. parryi* and *L. graveolens* (**Fig. 4**). It is not unusual to see *L. grayi* growing sympatric with these plant species throughout these regions, however, the Indra butterfly has never been observed using it as host. Instead, both butterfly subspecies preferentially chose *C. terebinthinus*, *L. junceum*, *L.* parryi and *L. graveolens* when present in mixed populations with *L. grayi*.

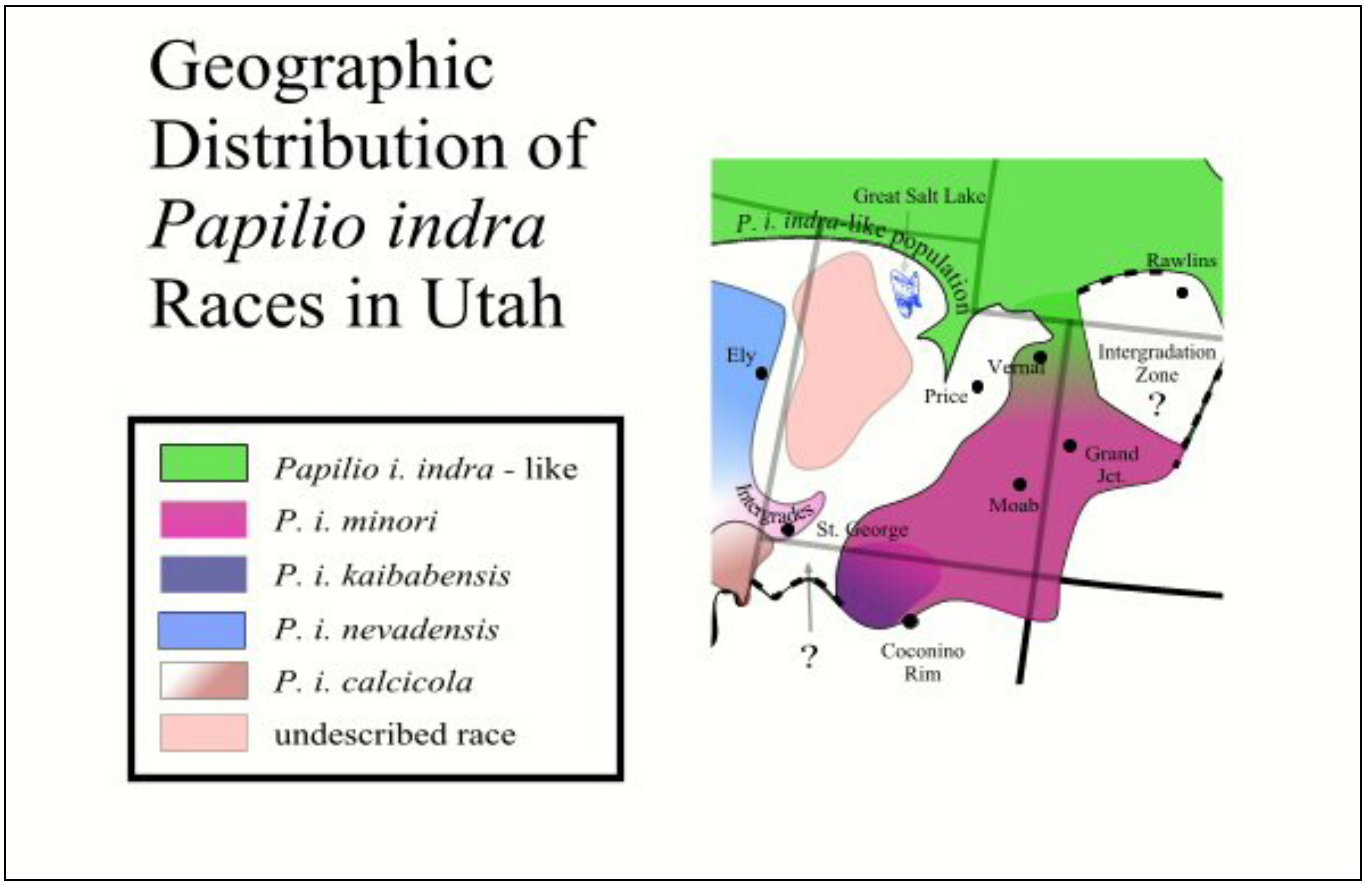

Fig. 4. Distribution of *P. indra* races in Utah.

***Papilio indra bonnevillensis* Whaley, Alexander & Stout – new subspecies**

ZooBank registration: urn:lsid:zoobank.org:pub:021FBED9-6B41-414D-A571-8C88A4654AFD

Adult characteristics. Ssp. *bonnevillensis* is similar in size and appearance to *P. indra calcicola* but with shorter tails and with more blue in the dorsal hindwings. Also, in *bonnevillensis* the dorsal hind wing black border (unlike calcicole) is far from the margin of the hind wing discal cell. Topotypical forewing length varies from 2.1 to 2.8 inches averaging 2.6 inches. The width of the cream bands is usually comparable to *calcicola* with the exception of a few specimens that have thin bands (superficially similar to *P. indra martini*) or very wide forewing bands (superficially similar to *P. indra fordi*) (**Plate 2, nos. 11-18**).

Also, forewing tips are “more pointed” or “less rounded” when compared with *P. indra indra*. Hind-wing tail lengths are shorter than *P. indra calcicola* where a few are basically “stubs” similar to nominate *indra* (**Plate 2, nos. 19-24**).

Larval characteristics. At the type locality fifth instars are black, with no bands or very small bands as found in nominal *indra* fifth instars (**Fig. 7**)**.** In most populations 50 to 75 percent of the fifth instars are all black with no bands (**Fig. 7**). When bands are present, they are pale neutral gray with a pink or purplish cast and are thinned out and/or incomplete in nearly all cases. Segmental spots are frequently the same color as the bands (Drum Mountains) while some have a slight yellow tint, and a few are yellow ocher. Earlier instars are black with the typical pattern of white spots but these are much reduced or frequently missing altogether (**Fig 6**). Some Bountiful Peak, UT specimens are also "pale horn color”. In most populations southward, 50 to 75% of the fifth instars (70% black from Drum Mountains) are all black with no bands. When bands are present they are pale neutral gray with a pink or purplish cast and are thinned out and/or incomplete in nearly all cases. Segmental spots are frequently the same color as the bands (Drum Mountains), some have a slight pale tint, and a few are yellow ochre.

Geographic Range and Life History. The range of *P. indra bonnevillensis* circumscribes remnants of Pleistocene Lake Bonneville restricting it to Utah's Great Basin limestone mountain ranges including the Dugway Range, Thomas Range, Little Drum Mountains, Topaz Mountain, House Range, Confusion Range, Wah Wah Mountains, Fish Springs Range, Rocky Range, Gilson and Canyon Mountains where *Lomatium depauperatum* grows between 4,300 and 6,500 feet elevation (**Fig 6**). There are other mountain ranges in Utah’s West Desert adjacent to these ranges that likely harbor populations of *Lomatium depauperatum* and *Papilio indra bonnevillensis* but they have not been thoroughly researched. Also, populations of *bonnevillensis* are considered hypothetical north of the Dugway Range in Southern Tooele County and north through Box Elder County mainly because the military base of Dugway Proving Grounds prohibits public access. Likewise, much of Box Elder County contains the Bonneville Salt Flats which is not suitable habitat. Efforts to find populations of *bonnevillensis* in NE Box Elder County in the Bovine Mountains and Grouse Creek Range have failed even though Whaley has found *L. depauperatum* growing there.

Because the distribution of *P. indra bonnevillensis* falls within the rain-shadow, consistent annual Spring flights of this butterfly can be less reliable. Because of successive dry winters and long-term drought, to survive these desert conditions, *P. indra bonnevillensis* pupae assess winter precipitation and do not emerge (or emerge poorly) following dry winters. Pupae remain in diapause through Spring, Summer, and Fall, reassessing the precipitation the following Winter and the cycle repeats. We found that some *P. indra* pupae can survive up to five years. In the House Range of Millard County, for several dry years prior to 2018, *P. indra bonnevillensis* was not seen on wing; but also, *Lomatium depauperatum* plants were water-stressed and were of smaller size. However, following a moderately wet winter in 2018 followed by an even wetter winter of 2019, *Lomatium depauperatum* recovered in size and *Papilio indra bonnevillensis* and *Papilio zelicaon* emerged and experienced very strong flights. Not only did *bonnevillensis* recover that spring; also, previously stressed populations of *Chlosyne leanira alma*, *Chlosyne acastus*, and *Euphydryas anicia wheeleri* were common on wing.

Earliest collection records for *P. indra bonnevillensis*: 27 March 1999 Prof. Whaley and freshman student Wilkinson at unnamed “hill” 5 km. S of Topaz Mountain, UT.

Type locality. The type locality of *P. indra bonnevillensis* is the Canyon Mountains, 4 miles ENE to 3.8 miles SE of Leamington, in Juab/Millard County, UT. Because Canyon Mountains precipitation is greater than precipitation in most of the West Desert mountain ranges ssp. *bonnevillensis* is on wing nearly

every year making it ideal for future research. Type specimens (Plate 1) will be donated to BYU's Monte L. Bean Life Sci. Museum, Provo, Utah.

Etymology. *Bonnevillensis* is the latinization of Lake Bonneville of the Pleistocene Epoch, remnants which covers large regions of western Utah where *bonnevillensis* is found (**Fig. 5**). We herein describe the new *Papilio indra* ecogeographical race which is restricted to remnants of Pleistocene Lake Bonneville in limestone rich mountain ranges of Utah's Great Basin.

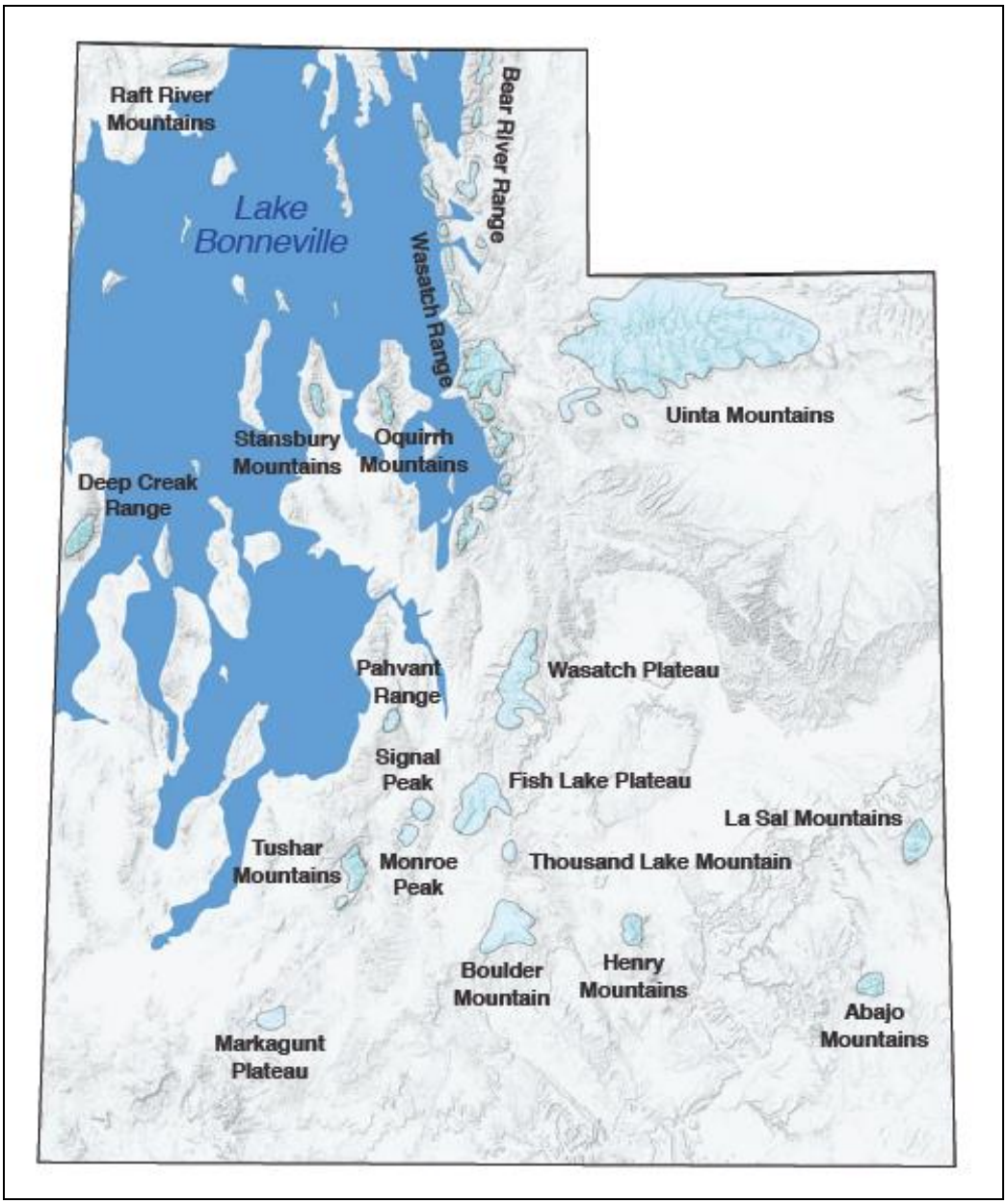

Fig. 5. Physiographic regions in Utah.

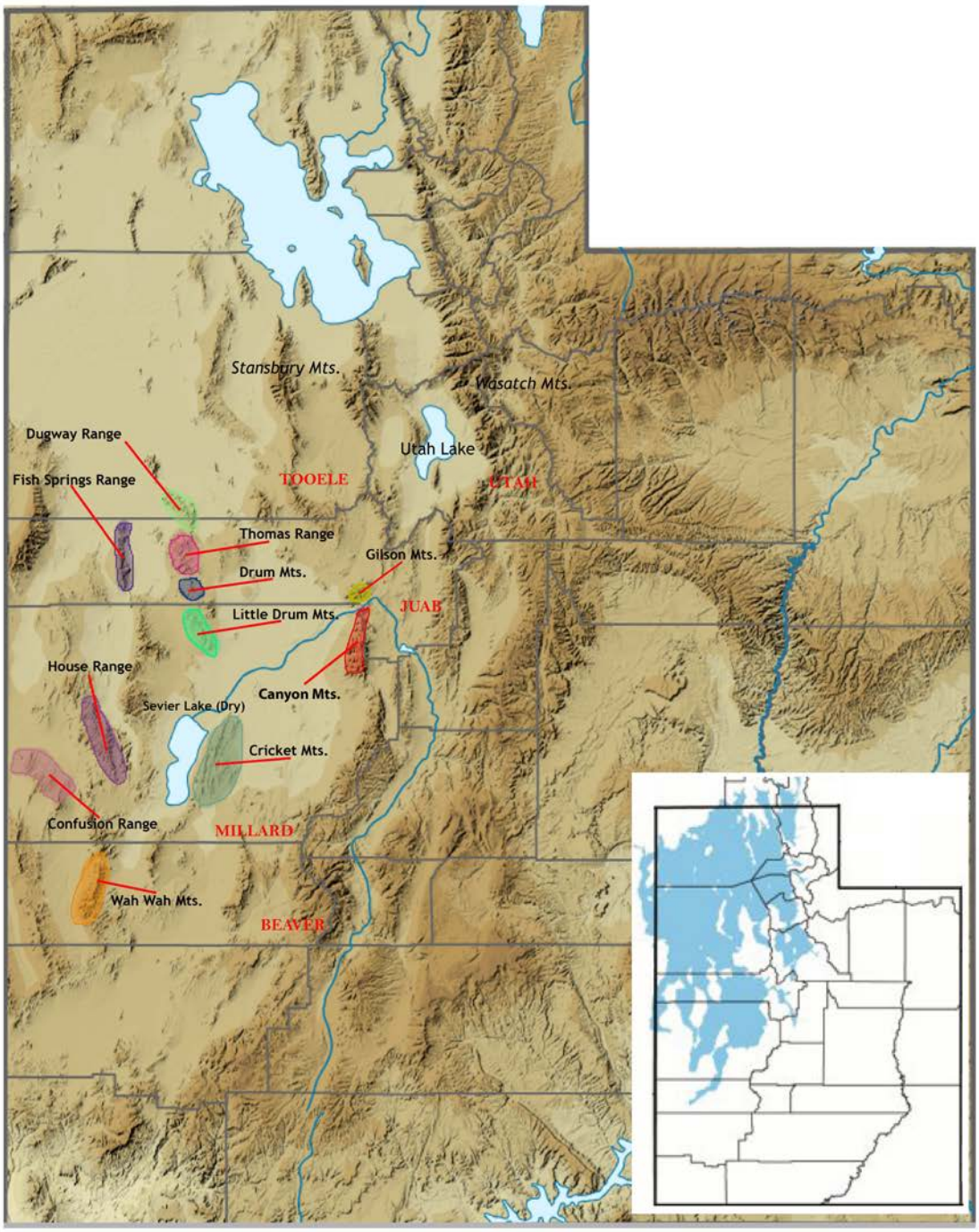

Figure 6a: (inset) Pleistocene Lake Bonneville
Figure 6b: *P. indra bonnevillensis* Documented Montane Range Distribution

Ovum--Canyon Mts.

Second instar--Canyon Mts.

Third instar--Canyon Mts.

Fourth instar--Canyon Mts.

Fifth instar--Canyon Mts.

Fifth instar--Confusion Range

Fifth instar--Canyon Mts.

Fifth instar--Confusion Range

Pupa--Canyon Mts.

Eclosed Adult--Canyon Mts.

Figure 7: *P. indra bonnevillensis* Photo Life History

ACKNOWLEDGMENTS

We greatly appreciate the recommendations of our anonymous peer reviewers. We thank Todd Stout for the excellent photographs attached to this work.

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PLATE 1

PLATE 1 *captions*

Papilio indra bonnevillensis

1. Male dorsal, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Female coll. 25 Apr 2019. Male eclosed 2 May 2020
2. Male ventral, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Female coll. 25 Apr 2019. Male eclosed 2 May 2020
3. Male dorsal, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Larva coll. 15 May 2019. Male eclosed 17 Apr 2020
4. Male ventral, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Larva coll. 15 May 2019. Male eclosed 17 Apr 2020
5. Male dorsal, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Larva coll. 4 May 2019. Male eclosed 12 Apr 2020
6. Male ventral, Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Larva coll. 4 May 2019. Male eclosed 12 Apr 2020
7. Male dorsal, Holotype Utah, Millard Co., Canyon Mountains, 0.4 miles South of UT Hwy 132. Female coll. 25 Apr 2019. Male eclosed 28 Apr 2020
8. Male ventral, Holotype Utah, Millard Co., Canyon Mountains, 0.4 mi South of UT Hwy 132. Female coll. 25 Apr 2019. Male eclosed 28 Apr 2020
9. Female dorsal, Utah, Millard Co. Canyon Mountains, 0.1 miles North UT Hwy 132. Female coll. 9 May 2019. Female eclosed 3 May 202
10. Female ventral, Utah, Millard Co. Canyon Mountains, 0.1 miles North UT Hwy 132. Female coll. 9 May 2019. Female eclosed 3 May 2020
11. Female dorsal, Allotype, Utah, Millard Co. Canyon Mountains, Leamington Pass Road. Larva coll. 22 May 2017. Female eclosed 11 May 2020
12. Female ventral, Allotype, Utah, Millard Co. Canyon Mountains, Leamington Pass Road. Larva coll. 22 May 2017. Female eclosed 11 May 2020
13. Female dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Female eclosed 24 Mar 1995
14. Female ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Female eclosed 24 Mar 1995
15. Female dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
16. Female ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
17. Female dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
18. Female ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
19. Female dorsal, Utah, Juab Co. Little Drum Mountins, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
20. Female ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Female eclosed 28 Feb 1994
21. Male dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Male eclosed 6 Mar 1993
22. Male ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Male eclosed 6 Mar 1993
23. Male dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Male eclosed 30 Mar 1994
24. Male ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Male eclosed 30 Mar 1994

PLATE 2

PLATE *2 captions*

Papilio indra bonnevillensis

1. Male dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1992. Male eclosed 8 Mar 1993

2. Male ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1992. Male eclosed 8 Mar 1993

3. Male dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Male eclosed 25 Mar 1994

4. Male ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. 8 May 1993. Male eclosed 25 Mar 1994

5. Male dorsal, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Male eclosed 9 Mar 1993

6. Male ventral, Utah, Juab Co. Little Drum Mountains, North side UT Hwy 174. Larva coll. May 1991. Male eclosed 9 Mar 1993

7. Female dorsal, Utah, Millard Co. House Range, NW side UT Hwy 50-6. Ovum coll. 2 May 2003. Female eclosed 18 Mar 2004

8. Female ventral, Utah, Millard Co. House Range, NW side UT Hwy 50-6. Ovum coll. 2 May 2003. Female eclosed 18 Mar 2004

9. Male dorsal, Utah, Millard Co. House Range, NW side UT Hwy 50-6. Ovum coll. 2 May 2003. Female eclosed 24 Mar 2004

10. Male ventral, Utah, Millard Co. House Range, NW side UT Hwy 50-6. Ovum coll. 2 May 2003. Female eclosed 24 Mar 2004

Papilio indra calcicola

11. Female dorsal, Utah, Washington Co. 4 miles North of St. George. Female coll. 15 Apr 2014. Female eclosed 30 Aug 2004

12. Female ventral, Utah, Washington Co. 4 miles North of St. George. Female coll. 15 Apr 2014. Female eclosed 30 Aug 2004

13. Female dorsal, Utah, Washington Co. 3 miles North of St. George. Larva coll. 18 Apr 1992. Female eclosed 7 Mar 1993

14. Female ventral, Utah, Washington Co. 3 miles North of St. George. Larva coll. 18 Apr 1992. Female eclosed 7 Mar 1993

15. Male dorsal, Utah, Washington Co. Yellow Knolls Ridge; 7.3 miles North of St. George Male coll. 8 April 1989

16. Male ventral, Utah, Washington Co. Yellow Knolls Ridge; 7.3 miles North of St. George Male coll. 8 April 1989

17. Male dorsal, Utah, Washington Co. 3 miles North of St. George. Coll. 13 Apr 1990.

18. Male ventral, Utah, Washington Co. 3 miles North of St. George. Coll. 13 Apr 1990.

Papilio indra indra

19. Male dorsal, Utah, Davis Co. Bountiful Peak; Wasatch Mountains; Larva coll. 17 July 1993. Male eclosed 21 May 1995

20. Male ventral, Utah, Davis Co. Bountiful Peak; Wasatch Mountains; Larva coll. 17 July 1993. Male eclosed 21 May 1995

21. Female dorsal, Utah, Salt Lake Co., 0.5 miles West Mt. Raymond; Wasatch Mountains; Female coll. 20 Jun 1990. Female eclosed 25 Apr 1992

22. Female ventral, Utah, Salt Lake Co., 0.5 miles West Mt. Raymond; Wasatch Mountains; Female coll. 20 Jun 1990. Female eclosed 25 Apr 1992

23. Female dorsal, Utah, Davis Co. Bountiful Peak; Wasatch Mountains; Larva coll. 17 July 1993. Female eclosed 13 Jul 1994

24. Female ventral, Utah, Davis Co. Bountiful Peak; Wasatch Mountains; Larva coll. 17 July 1993. Female eclosed 13 Jul 1994

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TILS Purpose

TILS is devoted to the worldwide collection of Lepidoptera for the purpose of scientific discovery, determination, and documentation, without which there can be no preservation.

TILS Motto

"As a world community, we cannot protect that which we do not know"

Articles for publication are sought

Manuscripts may deal with any area of research on Lepidoptera, including faunal surveys, conservation topics, life histories and foodplant records, matters of nomenclature, descriptions of new taxa, methods, etc. Taxonomic papers are particularly welcome. There are no publication charges for authors. Before submitting a manuscript, email **TTR editor, Harry Pavulaan, 606 Hunton Place NE, Leesburg, VA, 20176, USA** at intlepsurvey@gmail.com (cc: to harrypav@hotmail.com if you do not receive a reply within one week) to initiate discussion on how to best handle your material for publication, and to discuss peer review options.

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